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Original article

Can land crabs be used as a rapid ecosystem evaluation tool? A test using distribution and abundance of several genera from the Seychelles

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ABSTRACT

Habitat destruction and the introduction of exotic species are the primary causes of biodiversity loss in tropical island ecosystems. Conservation efforts on oceanic islands are often biased towards charismatic vertebrate faunas, neglecting invertebrate assemblages. We sampled the land crab community on five islands in the central Seychelles; in the intertidal zone, in the supralittoral zone and in nine different inland habitat types to explore the impacts of exotic vegetation and environmental variables on land crab abundance and community composition, and investigate whether land crabs can be used as a tool for the rapid assessment of habitat quality on tropical oceanic islands. We found that species richness and the abundance of the dominant ghost crab *Ocypode cordimana* was higher in native habitat types than habitats dominated by exotic vegetation. Available ground substrate suitable for burrowing may be a limiting factor for *O. cordimana* in exotic habitat types. *Coenobita rugosus*, the dominant crab in the supralittoral zone is largely absent where there is no supralittoral vegetation. These results suggest that land crabs could be reliable indicators of habitat quality on oceanic islands. The abundance of land crabs could be used in the rapid assessment of ecosystem perturbation and identification of sites requiring restoration or management.

1. Introduction

Oceanic islands are often priorities for conservation action owing to their high levels of endemism and continuing loss of habitats and species following anthropogenic activities (Myers et al., 2000). Habitat modification together with introductions of exotic species, are the primary threats to island biodiversity and indeed many other ecosystems (Brooks et al., 2002). These factors have, for example, contributed to the loss of more than 80 species of endemic land birds in Hawaii since human colonisation (Steadman, 1995), the high percentage (61%) of non-indigenous vascular plants in the Azorean archipelago (Silva and Smith, 2004) and the loss of over 40 percent of New Zealand's avifauna (Dowding and Murphy, 2001). On island archipelagos and many other ecosystems, conservation efforts have focused largely on the endemic avifauna and large land vertebrates.

The diverse Seychelles archipelago contains the only granitic islands in the Indian Ocean. These islands have been classified as a conservation priority owing to their high proportion of endemic taxa, many of which are threatened with extinction (Burgess et al., 2006). Extensive lowland forest clearance for agriculture since the 18th century has resulted in the extinction of at least three endemic bird species, localised extinctions of populations from many islands (Diamond, 1984) and the dominance of introduced plants in many habitats (Gerlach, 1993; Fleischmann, 1999). The restoration of native ecosystems, in conjunction with the eradication of invasive species is crucial to the conservation of island flora and fauna (Thorsen et al., 2000). Restoration programmes tend to be very costly however, depending on the interventions needed to rehabilitate degraded ecosystems. Field surveys represent the most significant cost in planning the restoration of island ecosystems in the Seychelles, accounting for approximately 15% of the total estimated cost of restoration programmes. Average survey costs across 11 potential islands was estimated at US $155 per ha (Henri et al., 2004). These costs could be reduced however, by the development of a method for rapid assessment of ecosystem state.

The extent to which invasive species and the associated changes to ecosystem structure has affected lesser known native species in the Seychelles has not been quantified. The impact of an infestation of the yellow crazy ant (*Anoplolepsis gracilipes*) on the community composition of ground-dwelling invertebrates on Bird Island, Seychelles, in 2000 highlighted the potential effects of invasive species on invertebrate populations. Larger decapod crustaceans were almost eliminated from the worst affected areas, with

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unknown effects on ecosystem function (Hill et al., 2003). The removal of the red land crab "*Gecarcoidea natalis*" by *A. gracilipes* in some areas of Christmas Island (105°40′E, 10°30′S), Indian Ocean, had cascade effects on populations of native species at multiple trophic levels (O'Dowd et al., 2003). This example highlights a paucity of information on the importance of invertebrate consumers in many island ecosystems and even less is known about the effects of habitat alteration on invertebrate communities and the associated implications for ecosystem functioning. On Christmas Island, red land crabs are found wherever the native rain forest is intact (Green, 1997), but the study does not quantify the extent to which habitat quality and non-native vegetation impacts land crab distribution and abundance. Little is known about the relative importance of potential factors limiting land crab distribution and abundance; along with biophysical factors (e.g. temperature, water availability), the presence of shade, suitable habitat for burrowing and habitat type are likely to be very important (Wolcott, 1988), but this has not been quantified. Dominance of non-native vegetation may affect land crabs through leaf litter depth and structure, available ground for burrowing and tree root structure. Tree roots provide habitat for burrowing and refuges for land crabs when inactive during the hottest part of the day (Wolcott, 1988).

Burggren and McMahon (1988a) broadly define land crabs as those showing significant behavioural, morphological, physiological, or biochemical adaptation permitting extended activity out of permanent water. Longevity and growth rates of terrestrial crabs are not known for many species due to a lack of information regarding moult frequency and increment. However, estimates of these parameters on the basis of relative growth of body dimensions and size at maturation for *Ocypode ceratophthalmus* have allowed the lifespan of this species to be approximated at two to three years (Burggren and McMahon, 1988b). A similar lifespan is expected for other *Ocypode* species. Following copulation and a period of egg incubation, the larvae of many terrestrial crabs, including *Ocypode*, *Coenobita* and *Geograpsus*, are released into a pelagic marine environment and are dispersed by ocean currents (Burggren and McMahon, 1988b).

On many tropical islands, land crabs occupy the top of the food web (Alexander, 1979). Crab detritivory affects nutrient cycling processes in some coastal tropical forest habitats and other effects on ecosystem functioning are likely (Kellman and Delfosse, 1993). For example, Micheli et al. (1991) estimated that soil turnover achieved by burrowing crabs in East Africa could displace and mix up approximately one quarter of the upper 20 cm of soil per year. The effects of the latter may include the enrichment of the soil by its oxygenation and the transport of organic material to the upper layers, which may increase the productivity of vegetation in mangrove marshes (Micheli et al., 1991). The effects of seedling predation by crabs on vegetation and plant communities have been quite widely documented; propagule predation by crabs strongly affected the establishment success of six out of nine mangrove species in Australia. These herbivores had a greater impact on initial recruitment than microhabitat resource effects (Clarke and Kerrigan, 2002). Sherman (2002) and Lindquist and Carroll (2004) suggest that land crabs (*Gecarcinus quadratus* and *Coenobita compressus*) influence seedling establishment and the composition of rain forest communities through differential predation in tropical forests of Costa Rica.

As the dominant consumer of most rain forest seeds and seedlings on Christmas Island, the red crab (*G. natalis*) may impede the establishment and recruitment of many plants including invasive species on oceanic islands (Green et al., 1997). The elimination of local red crab populations by the invasive *A. gracilipes* on Christmas Island resulted in an increase in seedling recruitment and a reduction in decomposition rates on the forest floor (O'Dowd et al., 2003). The potential for 'invasional meltdown' following the local extinction of crab populations suggests that land crabs are a potential keystone species in the tropical forests of oceanic islands (O'Dowd et al., 2003) and the functional group most influential to ecosystem functioning of rain forest habitat on Christmas Island (Green, 1997).

We suspect that if sensitive to habitat disturbance, land crabs could be good indicators of habitat quality on tropical islands as they fulfil several suggested critical criteria for indicator taxon (Caro and O'Doherty, 1999; Hilty and Merenlender, 2000): 1) the adults are relatively immobile on oceanic islands making them unable to escape adverse conditions; 2) but their larvae are dispersed widely by the sea enabling them potentially able to respond quickly to habitat improvement (Burggren and McMahon, 1988b); 3) they have high reproductive rates (Wolcott, 1988); 4) short generation times (Burggren and McMahon, 1988b); 5) can be found at relatively high densities (Green, 1997; Barros, 2001; Simões et al., 2001); 6) and are easy to find.

Very few studies have examined the community composition of land crabs in tropical island ecosystems, or investigated anthropogenic and environmental factors determining their distribution and abundance. Here we investigate the relationship between habitat quality and the abundance and species richness of land crabs on five islands in the Central Seychelles. Specifically, we (1) identified the species composition of land crab communities and (2) measured the impacts of exotic vegetation and environmental variables on land crab abundance and community composition, to investigate whether land crabs can be used as a tool for the rapid assessment of habitat quality on tropical oceanic islands.

2. Methods

2.1. Study site

Sampling was conducted between 14th April and 30th May 2006, on five small islands in the Central Seychelles Group: Cousin (04°20′S, 55°40′E, 29 ha), Cousine (04°20′S, 55°40′E, 26 ha), North (4°67′S, 55°17′E, 210 ha), Denis (3°80′S, 55°67′E, 140 ha) and Bird Island (3°43′S, 55°13′E, 70 ha) (Fig. 1). Islands were selected on the

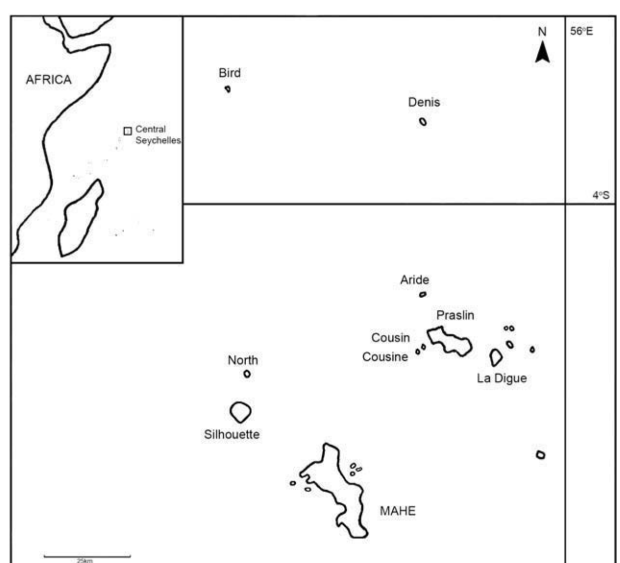

Fig. 1. The Central Seychelles island group and location of study sites within the archipelago.

basis of size, human population density, diversity of habitats, degree of degradation and accessibility.

Cousin Island is a Special Nature Reserve owned and managed by Nature Seychelles. A former coconut plantation, the island has been forested with native species since 1982, having been cleared of young coconuts and other invasive species from 1968 to 1970 (Komdeur and Pels, 2005). The island is now largely dominated by native species including: *Pisonia grandis*, *Morinda citrifolia*, and *Ochrosia oppositifolia* (Hill, 2002). Approximately 10 wardens are resident on Cousin Island with up to 80 tourists visiting the island six days a week throughout the year.

Cousine Island is a privately owned nature reserve with four tourist villas and less than 30 staff resident on the island. The vegetation on the hill area of the island has remained largely intact but the plateau was converted to plantation agriculture. A restoration programme has focused on the replanting of endemic species and the removal of exotics since 1995. The island is now covered in mixed native forest with no overall dominant species except for some small areas of *P. grandis* and *Pandanus* spp.

North Island is owned by a private company with 11 tourist villas and approximately 120 staff resident on the island. The majority of the vegetation of North Island was removed in the late nineteenth or early twentieth century for coconut plantation and fruit tree cultivation (Hill, 2002). The island has had a conservation program in place since 1997 although the vegetation is largely dominated by *Cocos* spp. and other invasive species.

Denis Island is a private coralline island resort with 25 tourist villas and approximately 80 staff resident on the island. The island was cleared and managed as a coconut plantation until the 1950s and was previously mined for guano. Although some natural vegetation remains, a restoration programme has been in place since 2000; 40 ha of the island has been set aside for conservation and is currently being cleared of *Cocos* spp. and other invasive plants.

Bird Island is a privately owned sand cay with 24 tourist chalets situated from the southern tip to the centre of the island, and approximately 40 resident staff. The northwest part of the island is set aside for the sooty tern (*Sterna fuscata*) colony, which is dominated by grassland and native shrubs. The island was under coconut plantation previous to 1973, the majority of which has since been felled to allow expansion of the sooty tern colony and construction of the tourist lodge.

2.2. Land crab survey

Surveys sampled three genera of land crabs: ghost crabs (Ocypodidae), hermit crabs (Coenobitidae) and Geograpsidae. Islands were stratified by habitat type using the classifications by Hill (2002), and sampling effort in each habitat type was proportional to the area of habitat. Some land crabs are more terrestrial whilst others require regular marine access. Sampling within habitats therefore necessitated a segmented transect approach, reflecting the differing distances of the target species from the shore and the three distinct environmental zones: the intertidal zone (upper and lower shore, determined by high and low tide), the supralittoral zone (0 m and 5 m from the top of the intertidal zone) and the inland zone (25 m, 50 m and 100 m from shore). The location of these sampling sites (segmented transects) within each habitat type was randomly selected using island maps with a grid overlaid. Sites were located at least 100 m apart to ensure that crabs were not sampled more than once as they are often highly mobile when foraging (Wolcott, 1988). Sampling was conducted within 4×4 m quadrats, sampling units of this size have been used to estimate the relative abundance of land crabs in previous studies e.g. Green (1997) and are an appropriate size to ensure individuals are only counted once.

Ocypodidae and Geograpsidae were sampled by counting burrows or individuals as they typically occupy only one burrow and may retreat into it if approached. The species inhabiting the burrows was identified if visible at the entrance or by static observation of the burrows until the crab emerged. Coenobitidae had emerged from daytime refuges by the time of sampling and could be counted and identified by static observation.

Islands were sampled in succession: Cousin Island from 14/04/06–20/04/06; Cousine Island from 22/04/06 to 30/04/06; North from 04/05/06 to 14/05/06; Denis from 18/05/06 to 25/05/06 and Bird from 27/05/06 to 30/05/06. Sampling in inland and supralittoral zones took place from 1630 h to 1830 h (before dark). As reported in previous studies of these taxa elsewhere (e.g. Barnes, 1997), land crabs became active on these Seychelles islands from approximately 1600 h onwards (earlier in cooler, wetter weather). In these zones it was not possible to determine land crab abundance earlier in the day, as the crabs spent daylight hours in inaccessible locations (Ocypodidae and Geograpsidae in burrows, Coenobitidae in rock and tree root crevices). Crab activity in the intertidal zone is determined predominantly by the tide more than the time of day, (SB pers. obs.) so quadrats in the intertidal zone were sampled just after daytime low tide, when ghost crab activity peaked.

We investigated the effects of inland habitat type (using the broad classifications of Hill, 2002) on land crab species richness and abundance by sampling the crab community in nine dominant inland habitat types : 1) *P. grandis* dominated native woodland, 2) mixed (species) native woodland, 3) coconut (*Cocos* spp.) dominated woodland, 4) *Calophyllum inophyllum* dominated woodland, 5) coconut and grassland, 6) *Casuarina equisetifolia* and grassland, 7) *C. equisetifolia* dominated woodland, 8) shrub and 9) grassland. When sampling crabs in the supralittoral and intertidal zones, the neighbouring inland habitat type was recorded as land crabs may travel to utilise the inland zone and could be influenced by inland habitat type. Marsh and mangrove habitat types were not surveyed as they occupy a very small proportion of island area (less than 3 ha in total).

P. grandis dominated native woodland, mixed native woodland, shrub and grassland, are all native habitats. *C. equisetifolia* dominated woodland, *C. equisetifolia* and grassland, and *C. inophyllum* dominated woodland contain both native and exotic species. *C. equisetifolia* is probably a naturalised species in the Seychelles but is not managed (Proctor, 1984). Coconut and grassland and coconut dominated woodland are both predominantly exotic habitat types. *Cocos nucifera* is native to Seychelles but was confined to the coastal fringes prior to its cultivation (Stoddart, 1984). However, other non-native species of coconut have also been introduced since human colonisation and the abandonment of many coconut plantations has resulted in *Cocos* spp. now occupying inland habitats previously dominated by other native vegetation.

Coenobitid crabs on North Island were strictly nocturnal, a behavioural trait not shown by populations on other islands. Daytime surveys found no active Coenobitids but tracks were present on the beach surrounding supralittoral vegetation. A nocturnal survey was carried out in the supralittoral vegetation from 2200 h to 2400 h from 08/05/06 to 09/05/06, at the same sampling points as the diurnal survey, to determine whether each species was actually absent from the island or just not detected during the daytime surveys.

2.3. Habitat assessment

Environmental variables were measured within each of the three zones to determine which features influence land crab species richness and abundance. Sampling units were classified into two simple altitudinal categories following Hill (2002): coastal plateau (<10 m above sea level) and hill (>10 m asl) to establish whether land crabs are affected by topographical features of the landscape. Hill areas are found on Cousin, Cousine and North Islands and are composed of rocky and bouldery soil.

The percentage cover of organic matter, bare soil, rock and ground flora was estimated visually within each quadrat. Canopy cover was calculated using a spherical densiometer (Lemmon, 1956) and depth of leaf litter recorded using a ruler (three measurements per quadrat). Soil penetrability was measured using the BJPS method of soil penetration (Jones and Reynolds, 1996); a pointed metal rod inserted within a metre long tube is dropped vertically into the ground from a standardised height. The depth to which the substrate was penetrated by the rod was then measured in mm with a tape measure. Soil types were identified from Seychelles soil maps (Unit K, Directorate of Overseas Surveys, 1966). Sampling units occurred on four different soil types: Seychelles red earth – uneroded phase; Shioya series (sandy soil); Jemo series and rocky/bouldery soil.

In the intertidal zone, different environmental parameters were measured to those in vegetated habitats. Geographical aspect (north, south, east, west) of the intertidal zone was measured using a map and compass. The width of the shore from the top of the intertidal zone to the sea was measured just after low tide shortly after sampling the crabs. The incline (slope) of the shore was measured using an inclinometer and measurements were sorted into three categories: steep, moderate and flat. Flat shores had an incline of 0–20°, moderate shores of 21–40° and steep shores of 41–90°.

2.4. Root systems of dominant tree species

To compare the size of the root systems between different tree species we measured the diameter at ground height (DGH) and diameter at breast height (DBH) of seven mature individuals of eleven dominant tree species in the Seychelles. We observed that in habitats where bare ground was inaccessible for burrow construction (e.g. excessive leaf litter build up) crabs were either not present or would utilise exposed tree roots for shelter and protection. We wanted to establish whether the area of exposed roots differed between tree species so that we could help determine whether certain tree species provided lesser quality habitat for land crabs than others.

2.5. Statistical analyses

Kruskal Wallis tests were used to compare median abundance of each species among the inland zone, supralittoral zone and the intertidal zone. These counts were Poisson distributed as many quadrats recorded no crabs. Relative density was used as a measure of abundance rather than absolute density, to account for variations in sampling effort between habitat types.

Non-metric Multidimensional scaling (MDS Clarke and Green, 1988) of the Bray Curtis similarity index was applied to counts of each species in each zone (inland, supralittoral and intertidal) to explore the similarity (species composition and abundance) between communities within each of these zones. The statistical significance of differences between zones was assessed using an analysis of similarities test (ANOSIM). Both of these analyses were conducted in Primer (v.5) (Carr, 1996).

The environmental distinctiveness of the intertidal zone, supralittoral zone and inland habitats from each other, necessitated slightly different environmental parameters to be measured in each zone (e.g. canopy cover and leaf litter depth were not measured in the intertidal zone and the width of the shore and geographical aspect for example, were not relevant in inland habitats). Separate analyses were therefore carried out to identify the effects of a range of environmental variables including: inland habitat type, percentage cover of organic matter, leaf litter depth and soil penetrability, on the relative density of the dominant species of land crab in each zone.

We used generalised linear models (GLMs) with Poisson errors using the R platform (Ihaka and Gentleman, 1996), correcting for over or underdispersion if necessary, to determine whether the abundance of each species and species richness is affected by the inland habitat type, island and several other environmental variables detailed above. Bonferroni corrected *a posteriori* analyses were carried out in R using the estimable function to determine where significant differences occurred. The Z statistic is reported for *a posteriori* analyses of data with Poisson errors and the T statistic is provided for *a posteriori* analyses of overdispersed or underdispersed data with Quasipoisson errors. A matrix plot produced in SPSS (v.13) tested all predictor variables for colinearity and found strongly colinear relationships between inland habitat type and both island and soil type: some habitats only occur on certain islands. Certain habitat types were also related to certain soil types (e.g. grassland habitats and beachcrest vegetation occurred only on Shioya soil). Analyses for each of the zones were therefore repeated three times to obtain the minimum adequate model with the best statistical fit, first with island as a predictor of land crab abundance and species richness, then inland habitat type and finally soil type. The inclusion of colinear factors in the same model may produce spurious relationships. Stepwise regressions were performed to produce minimum GLMs: non-significant factors were removed from the model step by step, with the least significant factor removed first.

Linear regression was performed to test the relationship between DBH of tree species and diameter at ground height (including roots). A positive relationship allowed the ratio of DBH to DGH to be calculated (as an index of above-ground root system size), to eliminate the effect that the size of the tree would have on the diameter of the roots. Analysis of variance then compared the ratios of the dominant tree species in Seychelles, to establish whether the trees have different sized above-ground root systems, which could be related to habitat quality for land crabs.

3. Results

3.1. Community composition

1026 land crabs of seven species were recorded during the study, including 918 Ghost crabs (Ocypodidae), 101 Hermit crabs (Coenobitidae) and seven yellow nippers (Geograpsidae). Three species of ghost crabs were recorded (*Ocypode cordimana*, *O. ceratophthalmus*, and *Ocypode ryderi*), together with three species of hermit crabs (*Coenobita brevimanus*, *Coenobita rugosus* and *Coenobita perlatus*).

ANOSIM demonstrated that there were no significant differences in community composition between zones (Fig. 2). However, Kruskal Wallis tests indicated that the abundance of the majority of crab species (*O. cordimana*, *O. ceratophthalmus*, *O. ryderi*, *C. rugosus* and *C. perlatus*) differed significantly between zones (Table 1). All subsequent analyses treat each zone separately and focus on the dominant species within each zone. *C. perlatus, C. brevimanus* and *Geograpsus crinipes* were not recorded at sufficient frequency to allow single species comparisons.

3.2. Inland zone

O. cordimana was the only species encountered frequently in the inland zone. Inland habitat type was the strongest predictor of

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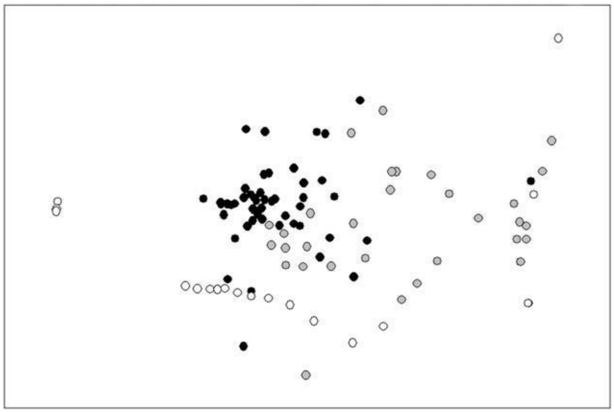

Fig. 2. MDS ordination of the abundance of seven species of land crabs in the three zones: intertidal, supralittoral and inland (Stress = 0.09, $P > 0.05$). Black circle = intertidal, grey circle = supralittoral zone, white circle = inland.

O. cordimana abundance and species richness, so island and soil type are excluded from the final model. The abundance of this species varied significantly with inland habitat type (Table 2; Fig. 3). *O. cordimana* were more abundant in native habitat types such as shrub, grassland and *P. grandis* dominated woodland than in habitats dominated by exotic trees such as *Cocos* spp. (Fig. 3).

Altitude and percentage cover of organic matter and rock in the inland zone also had significant effects on *O. cordimana* abundance (Table 2). On Cousine, this species was more abundant on the plateau ($P < 0.01$; mean ± SE: plateau 0.09 m^2 ± 0.01; hill 0.004 m^2 ± 0.003), whilst across all islands higher percentage cover by organic matter and rock had negative effects on *O. cordimana* abundance (organic matter $P < 0.05$, $t = -2.3$; rock $P < 0.01$, $t = -3.18$).

3.3. Supralittoral zone

O. cordimana, *O. ceratophthalmus* and *C. rugosus* were the most abundant species in the supralittoral zone (Table 1). In the supralittoral zone inland habitat type was the strongest predictor of *O. cordimana*, *O. ceratophthalmus* and *C. rugosus* abundance but island was the strongest predictor of species richness.

Inland habitat type was the only factor to exert a significant effect on *O. cordimana* abundance in the supralittoral zone (Table 3); *O. cordimana* was most abundant in the supralittoral zone bordering shrub and grassland habitat types and least abundant in the supralittoral zone bordering exotic woodland habitats and mixed native woodland (Fig. 4). In contrast, *O. ceratophthalmus* abundance in the supralittoral zone was not affected by inland habitat type (Table 3) but greater cover by bare soil did have a positive influence on *O. ceratophthalmus* abundance ($T = 2.76$, $P < 0.01$).

Table 1
Mean (±1 SE) relative density per m^2 of all species in each zone, with significant differences between zones (Kruskal Wallis).

	Inland	Supralittoral	Intertidal	X^2
O. cordimana	0.08 ± 0.01	0.06 ± 0.01	0.2 ± 0.02	53.19**
O. ceratophthalmus	0	0.03 ± 0.007	0.25 ± 0.02	171.96*
O. ryderi	0	0	0.04 ± 0.01	70.66**
C. rugosus	0.001 ± 0.001	0.04 ± 0.008	0.01 ± 0.003	37.75**
C. perlatus	0.001 ± 0.001	0.02 ± 0.008	0.003 ± 0.002	10.25*
C. brevimanus	0.001 ± 0.001	0.002 ± 0.001	0	2.79
G. crinipes	0.001 ± 0.001	0.001 ± 0.001	0.002 ± 0.001	0.05

**$P < 0.01$.
*$P < 0.05$.

Table 2
Factors affecting the abundance of *O. cordimana* in the inland zone (GLIM).

	df	*O. cordimana* LRX^2
Inland habitat type	8	126.58***
Altitude	1	7.18**
% cover organic matter	1	5.61*
% cover rock	1	13.4***

*** = $P < 0.001$.
** = $P < 0.01$.
* = $P < 0.05$.

C. rugosus abundance in the supralittoral zone was also significantly affected by the inland habitat type (Table 3). This species was most abundant in the supralittoral zone that bordered coconut dominated exotic woodland, *C. equisetifolia* dominated exotic woodland and *P. grandis* dominated native woodland (Fig. 4). *C. rugosus* was absent where there was no supralittoral vegetation (Fig. 5), and deep leaf litter and greater coverage by rock had a negative effect on *C. rugosus* abundance (Table 3).

Cousine Island had lower average species richness per m^2 than all the other islands (Fig. 6) but fewer species were recorded in the supralittoral zone of Bird Island (North 7; Denis 7; Cousin 6; Cousine 6; Bird 4). The presence of supralittoral vegetation significantly increased land crab species richness in the supralittoral zone (Fig. 5). Leaf litter depth significantly affected species richness with fewer species occurring in deep leaf litter ($Z = -1.998$, $P < 0.05$).

3.4. Intertidal zone

In the intertidal zone island was the strongest predictor of all three *Ocypode* species; inland habitat type was therefore excluded from the final model. The abundance of *O. cordimana*, *O. ceratophthalmus* and *O. ryderi* was affected by different factors (Table 4). *O. cordimana* were less abundant on Denis Island than all the other islands (Fig. 7), *O. ryderi* was more abundant in the intertidal zones of Bird, Denis and Cousine Islands than on Cousin and North Islands (Fig. 7).

O. cordimana and *O. ryderi* were more abundant on the upper shore than the lower shore (*O. cordimana*: $P < 0.01$; upper

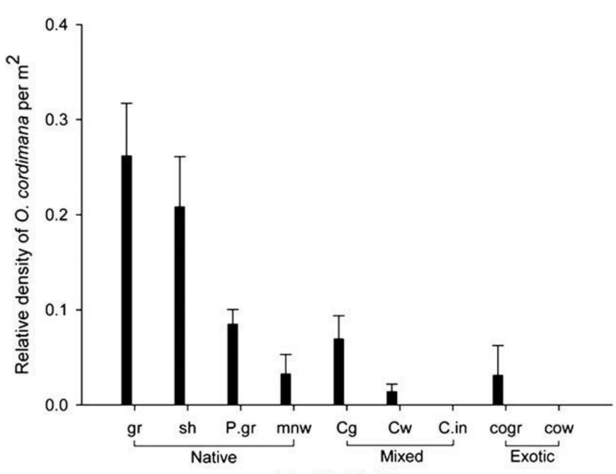

Fig. 3. Effect of inland habitat type on the relative density (mean ± 1 SE) of *O. cordimana* in the inland zone. gr = grassland, sh = shrub, P.gr = *P. grandis* dominated native woodland, mnw = mixed native woodland, Cg = *C. equisetifolia* and grassland, Cw = *C. equisetifolia* dominated woodland, C. in = *C. inophyllum* dominated woodland, cogr = coconut and grassland, cow = coconut dominated woodland.

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Table 3
Factors affecting the abundance of dominant species and species richness in the supralittoral zone (GLIM).

		O. cordimana	*O. ceratophthalmus*	*C. rugosus*	Species richness
	df	LRX^2	LRX^2	LRX^2	LRX^2
Island	4	–	–	–	9.77*
Inland habitat type	8	50.09***	0	109.04***	–
Leaf litter depth (mm)	1	0	0	14.25***	4.49*
% cover bare soil	1	0	7.09**	0	0
% cover rock	1	0	0	9.47**	0
Supralittoral vegetation	1	0	0	63.62***	5.52*

*** = $P < 0.001$.
** = $P < 0.01$.
* = $P < 0.05$.
NB. Inland habitat type and island are colinear, only the strongest predictor is included in the final model for each response.

0.23 m^2 ± 0.02; lower 0.13 m^2 ± 0.03; *O. ryderi*: $P < 0.001$; upper 0.07 m^2 ± 0.02; lower 0.02 m^2 ± 0.01) and *O. cordimana* was found at a greater density per m^2 on narrower than wide shores ($T = 2.13$, $P < 0.05$).

O. cordimana preferred steep shores to flat shores ($P < 0.001$; steep 0.29 m^2 ± 0.04; flat 0.15 m^2 ± 0.03) and *O. ceratophthalmus* was less abundant on Denis Island than on Bird, Cousin and Cousine (Fig. 7) This species occurred at higher frequencies on steep and moderate shores than flat shores ($P < 0.001$; steep 0.24 m^2 ± 0.03; moderate 0.27 m^2 ± 0.04; flat 0.11 m^2 ± 0.04).

O. ryderi was more abundant on north and east facing shores than west facing shores ($P < 0.001$; north 0.1 m^2 ± 0.03; east 0.08 m^2 ± 0.03; west 0.02 m^2 ± 0.01).

3.5. Root systems of dominant tree species

Tree DBH was significantly related to DGH, which included external root cover ($R^2 = 0.798$, $P < 0.001$). Tree species differed significantly in the extent of exposed root coverage ($F = 4.21$, df = 10, $P < 0.001$). *Cocos* spp. had the highest ratio of DBH to DGH of the inland tree species and therefore a lesser exposed root system than that of *Terminalia catappa*, *C. equisetifolia*, *P. grandis* and *O. oppositifolia*, which are all native species with the exception of *C. equisetifolia* ($P < 0.01$; *Cocos* spp. 0.76 ± 0.05; *T. catappa* 0.31 ± 0.16; *C. equisetifolia* 0.23 ± 0.06; *P. grandis* 0.21 ± 0.04; *O. oppositifolia* 0.31 ± 0.13).

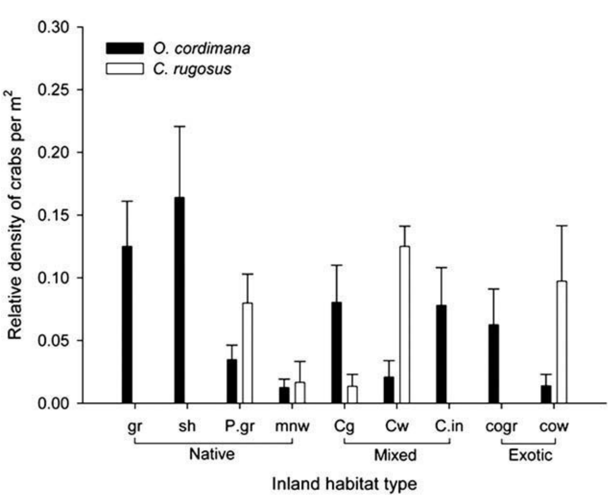

Fig. 4. Mean relative density (mean ± 1 SE) of *O. cordimana* and *C. rugosus* in the supralittoral zone, adjacent to different inland habitat types.

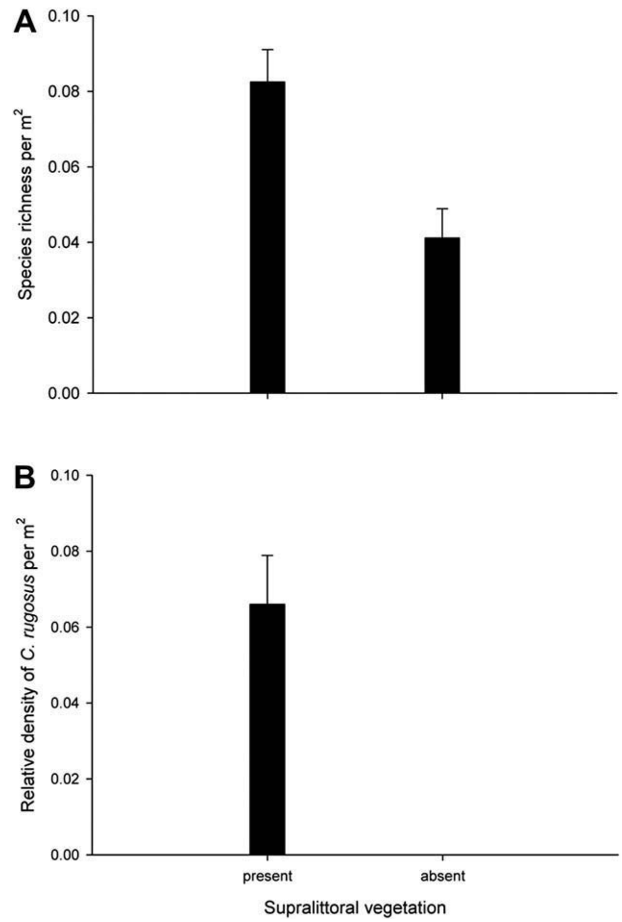

Fig. 5. Mean relative density (mean ± 1 SE) of A) *C. rugosus* and B) species richness in the supralittoral zone, with and without supralittoral vegetation.

C. inophyllum is a native inland tree species but this had a significantly higher DBH to DGH ratio and therefore less exposed roots, than *C. equisetifolia*, and *P. grandis* ($P < 0.05$; *C. inophyllum* 0.61, ±0.13; *C. equisetifolia* 0.23 ± 0.06; *P. grandis* 0.21 ± 0.04).

4. Discussion

Our results demonstrate that certain species of land crab are affected by habitat quality. The prevalence of exotic flora had negative effects on the abundance of the dominant land crab in the inland zone and the lack of supralittoral vegetation resulted in the absence of the dominant species in this zone. These results support the hypothesis that land crabs could be used as reliable indicators of habitat quality on oceanic islands.

4.1. Community composition

The seven species of land crab found on the five Seychelles islands sampled occur from the Western Indian Ocean to the eastern part of the Indo-west Pacific Region (e.g. Hawaiian Islands) (Haig, 1984). Although we found no evidence for distinct land crab communities across different terrestrial zones, relative abundance of different species varied between these zones. For example, *O. ryderi* and *O. ceratophthalmus* were predominantly found in the intertidal zone and *C. rugosus* in the supralittoral zone. Small community size, the occurrence of one or two less common species in more than one zone and the universal distribution of

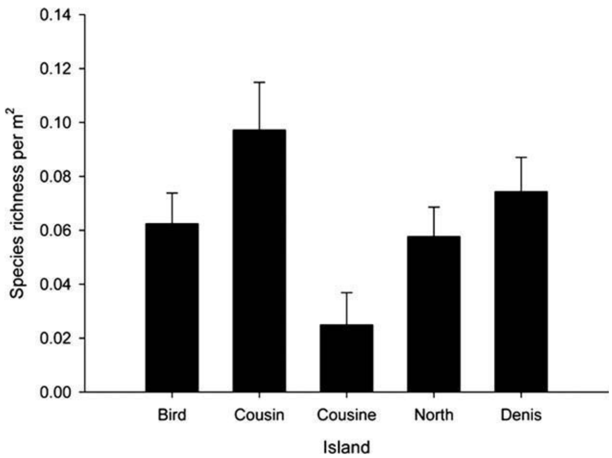

Fig. 6. Mean species richness per m^2 (mean ± 1 SE) in the supralittoral zone of each island.

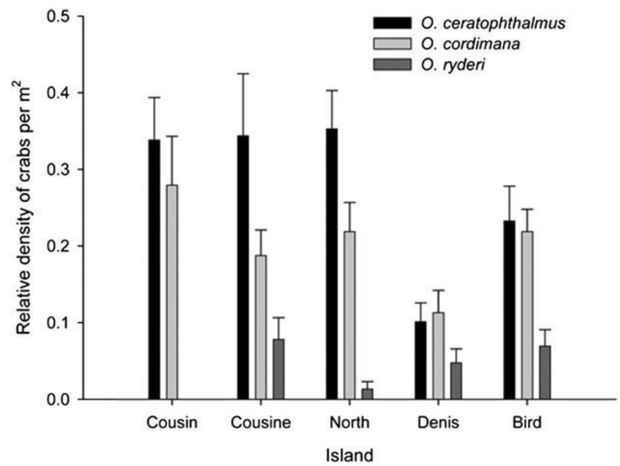

Fig. 7. Mean relative density (mean ± 1 SE) of Ocypodidae in the intertidal zone of each island.

O. cordimana probably account for the lack of significant difference in community composition between zones.

4.2. Inland zone

Our study suggests that exotic vegetation has a negative effect on land crab abundance in the inland zone. Similar results were found for red land crabs on Christmas Island where crab abundance declined sharply from the forest to disturbed areas (O'Dowd and Lake, 1991), and this disturbance affected their patterns of migration (Adamczewska and Morris, 2001). Conversion of mangroves to banana and coconut plantations in South America was responsible for declines in another species of land crab, *Cardisoma guanhumi* (Wolcott, 1988). Seychelles Orthopteroids exhibit similar habitat preferences; most of the endemic species are confined to remnant areas of native vegetation (Matyot, 1998). Exotic vegetation may provide sub-optimal habitat for land crabs (e.g. for feeding and cover) compared to native vegetation. Native invertebrates on another Seychelles island, Mahé, are largely unable to feed on the locally dominant, exotic plant *Memecylon floribundum*, reducing invertebrate species in *M. floribundum* dominated habitat (Gerlach, 1993).

The three native habitat types which supported the greatest abundance of land crabs were also the locations of the largest breeding colonies of seabirds. The grassland and shrub habitats on Bird Island support over 700,000 pairs of sooty terns (*S. fuscata*) whose eggs, guano and carcasses represent a substantial food resource for *O. cordimana*. Native *P. grandis* woodland on Cousin and mixed native woodland on Cousine also support large breeding colonies of seabirds. However, whilst *O. cordimana* is abundant on Cousin it is not very common on neighbouring Cousine, suggesting that food availability is not the only factor influencing *O. cordimana* abundance in native habitats.

Available burrowable substrate may limit *O. cordimana* distribution in exotic habitat types, as suggested in an earlier review of land crab biology (Wolcott, 1988). Sherman (2002) observed that in areas of forest with few or no burrows, crabs congregated at the base of trees and buttress roots. *O. cordimana* was more abundant where bare soil was available for burrowing, but in native habitats where ground coverage by organic matter was high *O. cordimana* may have been able to persist in these circumstances by burrowing under roots of native tree species. However, in exotic habitats *O. cordimana* are unable to burrow under tree roots as *Cocos* spp. and *C. inophyllum* do not have extensive exposed root systems. *O. cordimana* was also scarce in *C. inophyllum* and *C. equisetifolia* dominated mixed woodland where *Cocos* spp were also prevalent. The removal of *Cocos* spp. from inland habitats to allow regeneration of natural vegetation would very probably increase land crab abundance.

On Cousine Island, land crabs were scarce on the plateau despite good mixed native woodland cover. This may be due to the disturbance and barrier to dispersal imposed by the raised concrete paths which traverse the island. *O. cordimana* in Australia preferred to dig their burrows in areas away from human disturbance. The abundance of widely distributed ghost crabs was suggested as a rapid assessment indicator of human disturbance on sandy beaches in New South Wales, Australia (Barros, 2001). Our results indicate that *O. cordimana* is also a reliable indicator of inland habitat quality in the Seychelles and similar species could be used as indicators of habitat quality on other tropical islands.

4.3. Supralittoral zone

O. cordimana, *O. ceratophthalmus* and *C. rugosus* are the most abundant species in the supralittoral zone, as reported in previous studies of the Seychelles and Mozambique, (Haig, 1984; Anderson, 1993; Barnes, 1997). *O. cordimana* was more abundant in the supralittoral zone bordering native habitat types such as native grassland and shrub, relatively abundant bordering habitats with some grassland and least abundant in the supralittoral zone bordering inland habitats dominated by exotic woodland, but also in mixed native woodland. The low abundance of *O. cordimana* in mixed native woodland is most likely due to an island effect as this habitat is found on Cousine where disturbance is common in the supralittoral zone. These results suggest that *O. cordimana* present

Table 4
Factors affecting the species richness and abundance of dominant species in the intertidal zone (GLIM).

		O. cordimana	*O. ceratophthalmus*	*O. ryderi*
	df	LRX^2	LRX^2	LRX^2
Island	4	37.88***	44.14***	35.91***
Shore position	1	12.06***	0	14.68***
Geographical aspect	6	0	0	43.48***
Shore width	1	4.92*	0	0
Slope	3	26.34***	18.01***	0

*** = $P < 0.001$.
** = $P < 0.01$.
* = $P < 0.05$.

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in the supralittoral zone also utilise inland habitats where suitable and that exotic woodland dominated by *Cocos* spp. is a particularly unfavourable habitat for *O. cordimana*. Ghost crabs remain close to their burrow during the day but range to feed over much larger areas at night, and will also forage by day in areas undisturbed by humans (Wolcott, 1988). Conversely, *C. rugosus* was more abundant in the supralittoral zone bordering habitats dominated by exotic species such as *Cocos* spp. and *C. equisetifolia* but also in *P. grandis* dominated native woodland. The absence of *C. rugosus* from shrub and native grassland is more likely due to island effects than habitat type. These two habitats occurred on Bird Island where the abundance of *Coenobita* was very low overall. These results support previous studies suggesting that *C. rugosus* occurs across a range of habitat types (Barnes, 1997). The abundance of *O. ceratophthalmus* in the supralittoral zone was not affected by the inland habitat type; this species is predominantly an intertidal and supralittoral species (Haig, 1984).

The presence or absence of supralittoral vegetation did not affect *Ocypode* abundance but *C. rugosus* relied heavily on supralittoral vegetation areas. Supralittoral vegetation and its associated leaf litter, provides shelter and protection from the heat for Coenobitid crabs during the day (Wolcott, 1988; Barnes, 1997), a function that burrows fulfil in Ocypodids. Barnes (1997) found that protection and cover provided by different habitat types influenced activity patterns of hermit crabs on the Quirimba archipelago, Mozambique. Land crab communities on islands with a paucity of supralittoral vegetation may benefit from the replanting of native vegetation along the coastal fringe.

Cousine Island had lower average species richness per m^2 than the other islands, which may be due to localised disturbance, as discussed previously. Bird Island had the lowest recorded crab species richness overall; only one individual Coenobitid (*C. rugosus*) was recorded. The recent yellow crazy ant (*A. gracilipes*) infestation on Bird Island had adverse effects on larger decapod crustacea (Hill et al., 2003) but Coenobitids appear to have taken longer to recover from this infestation than Ocypodids. *A. gracilipes* similarly eliminated the red land crab from infected areas on Christmas Island (O'Dowd et al., 2003).

4.4. Intertidal zone

As found in other localities (Simões et al., 2001), land crab abundance was highest in the intertidal zone, possibly due to greater resource availability. The tide line offers a significant source of diverse nutrient inputs and organic matter and strand-line carcasses of birds and marine fauna can form a significant part of land crab diet (Alexander, 1979; Burggren and MacMahon, 1988b; Anderson, 1993).

Ocypodids dominated land crab communities in the intertidal zone with island emerging as the most significant factor influencing their abundance. *O. cordimana* and *O. ceratophthalmus* were significantly less abundant on Denis than any other island. *O. ryderi* was not sampled on Cousin and was relatively uncommon on North Island.

O. cordimana and *O. ceratophthalmus* were more abundant on steep compared to flat shores, as found in previous studies (Anderson, 1993). It may be more difficult to dig and maintain a burrow on a flat shore than a steep sloping shore. *O. cordimana* and *O. ryderi* were more abundant on the upper shore than the lower shore. *O. ceratophthalmus* exhibited no preference for shore position. The abundance of *O. ryderi* was influenced by geographical aspect, with greater numbers occurring on shores facing east and north than those facing west.

The percentage cover of organic matter on the shoreline did not affect the abundance of any of the Ocypodidae which have diverse diets and are therefore not dependent upon organic matter as a food source (Burggren and MacMahon, 1988b).

This study is one of the first to investigate the effects of habitat modification and exotic vegetation on land crab community composition and abundance, across several islands.

Our results suggest that the dominance of exotic vegetation and loss of native vegetation have negative effects on the abundance of some species of land crabs. Similar observations have been made in other island ecosystems (O'Dowd and Lake, 1991; Wolcott, 1988). The universal distribution of *O. cordimana* from the coast to inland habitats and its sensitivity to habitat type and disturbance leads us to believe that this species and other common species like it, may be a useful indicator of habitat quality in the Seychelles and on other tropical oceanic islands, allowing the rapid assessment of ecosystem degradation and the identification of areas in need of restoration. The strong dependence of hermit crabs, particularly *C. rugosus*, on intact native supralittoral vegetation, suggests that this species could act as a useful indicator of an intact ecotone; the absence of this species indicates that the supralittoral zone is of poor quality or absent and therefore the ecotone from intertidal zone to the forest is disrupted.

Based on the results of this study, it is possible to extrapolate a threshold density of *O. cordimana* in the inland zone, below which may indicate a low habitat quality. *O. cordimana* were most abundant in the native grassland, shrub, *P. grandis* dominated woodland (Cousin Island only) and *C. equisetifolia* and grassland habitat, at densities of 0.26 m^2, 0.21 m^2, 0.08 m^2 and 0.11 m^2 on average, respectively. Average density in remaining mixed and exotic habitat types were lower than 0.04 m^2 and 0 in some cases. We tentatively suggest that a threshold density of 0.05 m^2 would suggest poor inland habitat quality, if no other limiting factors are apparent (e.g. exploitation). Further research is required however, before this tool for rapid ecosystem assessment can be utilised. The extent to which land crab populations fluctuate naturally and how these fluctuations may affect the use of land crabs as indicator species, needs to be determined.

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